

A Phylogenetic Study of the Lateral Head, Neck and Prothoracic Regions in Some Apterygota and Lower Pterygota.*

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(Plate XXVII.)

Of the eight groups of lower Pterygotan insects here discussed, the Plecoptera are structurally the most similar to the Lepismids, and have apparently departed much less than the typical Blattids have from the ancestral condition of the Pterygota in general. Together with the Ephemeroidea, the Plecoptera are undoubtedly the lowest living winged insects, and, since the Lepismids (i. e. such forms as *Lepisma*, *Nicoletia*, etc.) form a sort of "connecting link" between the lower Pterygota and the more primitive Apterygotan forms (such as *Campodea*, *Japyx*, etc.) it is preferable to begin a study of the groups in question with a comparison of the conditions found in the Lepismids and Plecoptera.

In comparing the heads of the Lepismids (Plate XXVII, Fig. 1), the Blattids (Fig. 2), and an immature Plecopteron (Fig. 4), it is at once apparent that the Plecopteron is structurally much nearer the Lepismids than the typical Blattids are. Thus, in both Lepismids (Fig. 1) and Plecoptera (Fig. 4) the head is markedly prognathous (i. e. mouthparts directed forward), while in the typical Blattids (Fig. 2) the head is markedly opisthognathous (i. e. mouthparts directed backward). I am not sufficiently familiar with the Blattid group to know what extremes of variation are to be found among these insects, but, although some Blattids which I have not seen may also have heads of the prognathous type, it is nevertheless true that the condition depicted in Fig. 2 may be taken as typical for the Blattid group in general, in the following discussion.

The head contour is essentially similar in both Lepismids and the Plecopteron (Figs. 1 and 4); but the outlines of both heads differ very markedly from that of the Blattids (Fig. 2). Furthermore, the nature of the labium, and its mode of attach-

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ment to the head is much more "Lepismid-like" in the Plecopteron (Fig. 4) than in the Blattids (Fig. 2). In the same way the location of the "compound" eyes, and the position of the antennae are quite similar in the Lepismids and Plecopteron; but both differ strikingly from the Blattids in these respects. The clypeus and labrum also, are more alike in Lepismids and the Plecopteron, than these structures are in the Lepismids and Blattids, and the mandible of the Plecopteron is nearer the Lepismid type than the Blattid mandible is. In other words, the evidence to be gained from a comparative study of the external morphology of the head, would point to a close relationship between the Lepismids and the Plecoptera, and a much more distant relationship between the Blattids and Lepismids.

In taking up a consideration of the neck and thoracic regions in the Lepismids one finds (as might be expected) that the Lepismids have retained a condition resembling that found in the lower Apterygotan forms (such as *Japyx*, *Eosentomon*, etc.) rather than such a condition as occurs in the Pterygotan insects. The thoracic sclerites of *Japyx*, *Eosentomon*, etc., have been homologized in a paper dealing with the nature of the neck region of insects in general (which will shortly appear,* in the "Annals of the Entomological Society of America"), so that it is unnecessary to describe them here, since one may simply compare the accompanying figure of *Lepisma* (Fig. 1) with those of *Japyx*, *Eosentomon*, etc., in the aforementioned article. I would call attention, however, to the anterior transverse pronotal sclerite designated as "Pt" in Fig. 1. This sclerite is clearly the homologue of the transverse pronotal sclerite labeled "Pt" in Figs. 9 and 7; and it is in the tergal region that the Lepismids apparently approach the condition found in certain lower Pterygota, more closely than in any other thoracic structures.

The trochantin-like region "abc" (termed the "eutrochantin" in the paper referred to above) of the Lepismids (Fig. 1) is also somewhat similar to that found in Figs. 6 and 7, since it

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intervenes between the coxa and the true pleural sclerites; but the remainder of the prothoracic sclerites of the Lepismids are somewhat different from the typical sclerites of the lower Pterygotan forms. In this respect, *Nicoletia* would have been a better insect than *Lepisma* for a comparative study of the thoracic region, but I have hesitated to spoil my only specimen of *Nicoletia* by subjecting it to the staining process with nitrate of silver, etc., which is necessary to differentiate the sclerites from the membrane in these weakly pigmented forms.

There are two principal types of head found among the Apterygotan insects, namely the broad, flattened type, occurring among certain Lepismids, etc., and the more pear-shaped type, occurring in *Japyx*, etc. I find these two types represented among the Myriopods (*sensu lato*) and also among the Crustacea, so that these two types were apparently differentiated at a very early stage of development, and both were doubtless present among the first insects to be evolved. In fact, I believe that flat, broad-bodied forms as well as the more cylindrical, slender-bodied forms occurred among the ancestral insects (for such types also occur among the Crustacea, etc.), so that it is incorrect to say that the original insects were of this or that type, since *several* types must have been in existence at the very beginning of the development of insects. It is thus evident that insects are not the product of one type of ancestral forms alone, but the ancestral insects doubtless differed as much (if not more) among themselves as the modern representatives of the different families composing an order of insects differ among themselves.

It is undoubtedly true that throughout the animal kingdom, many living forms have departed but little from the ancestral condition characteristic of the early stages in the development of other living groups, and are fully as instructive as fossil forms are, in furnishing us with connecting links between many of the greater groups of the animal kingdom (such, for example, as the living Dipnoi, which furnish us with intermediate forms annectent between the fishes and Amphibia). In the same way, certain living insects have departed but little



LATERAL HEAD AND PROTHORACIC REGIONS.—CRAMPTON.

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| 1. <i>Lepisma</i> . | 2. <i>Periplaneta</i> . | 3. <i>Termea</i> . |
| 4. <i>Pteronarcys</i> . | 5. <i>Echinosoma</i> . | 6. <i>Embia</i> . |
| 7. <i>Capnia</i> . | 8. <i>Timema</i> . | 9. <i>Grylloblatta</i> . |

from the condition characteristic of the ancestors of certain other hexapodan groups, and, to my mind, the study of recent forms is even more instructive than the study of fossil insects, from the phylogenetic standpoint, since we are able to compare together more detailed structures in living forms, than it is possible to do in the distorted and usually imperfectly preserved fossil forms, the most of which are practically as highly specialized along their own lines of development as the most primitive of living forms are!

In the interesting insect *Grylloblatta campodeiformis* Walker we hold the key to the genealogy of the Orthopteroid insects (such as the Tettigonids, Gryllids, Locustids, etc.) and any attempt to trace the ancestry of these Orthopteroid forms, in which the evidence of affinities with the lower groups, furnished by the study of *Grylloblatta*, is ignored, is foredoomed to failure. On this account, I would present some of the evidence of relationship gained from a comparative study of the Grylloblattids and Embiids, since I am convinced that the Grylloblattids are extremely closely related to the Embiids, and are therefore ultimately to be derived from Plecoptera-like ancestors (since the Embiid line of development parallels that of the Plecoptera more closely than any of the lowest Pterygotan forms).

In an article dealing with the antennae of the Grylloblattids and Embiids, which will shortly appear* in the Canadian Entomologist, I have pointed out the astonishing similarity in the antennae of these two groups of insects—a similarity shown not only in the close agreement in the number of antennal segments, but which extends even to the more minute details of relative size and outline in the individual segments of the antennae in the two groups. On the other hand, the antennae of both Embiids and Grylloblattids are entirely different from those of the typical Blattids in regard to precisely those features wherein they are most similar to one another! In the present paper, I would endeavor to demonstrate that the remarkable

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similarity between the antennae extends to the neck plates, and other structures as well, in the Embiids and Grylloblattids, and in these features also, the Grylloblattids differ from Blattids (which some investigators would consider as their nearest relatives).

In conformity with the general depressed condition of the body, the head of *Embia* (Fig. 6) is somewhat flattened, but aside from this fact, and the modifications which the Embiids have developed along their own lines, the head of a Grylloblattid (Fig. 9) is somewhat like that of an Embiid (although both differ from the Blattids in this respect) and is quite like that of the Phasmid *Timema* (Fig. 8) in outline. Not only are the heads of the Grylloblattids and Phasmids more prognathous, like that of an Embiid (while the head of a Blattid is more opisthognathous), but the outline of the compound eyes, their extent upward along the sides of the head, the point of attachment of the antenna in relation to the eyes and to the base of the mandibles, etc., are infinitely more like those of an Embiid in the Phasmids and Grylloblattids, than they are like those of a Blattid, as may readily be seen by comparing Figs. 8 and 9 with Fig. 6 and then with Fig. 2.

The agreement in structure between the antennae of *Grylloblatta* and *Embia* is extremely striking, but the similarity between the neck plates and prothoracic sclerites of these insects is no less remarkable (and in these points of similarity both Embiids and Grylloblattids differ markedly from the condition found in the Blattids). If one will cover the heads of the insects shown in Figs. 6 and 9, so as to concentrate his attention upon the plates behind the head region, he will be immediately struck with the remarkable agreement between the sclerites of the Grylloblattids and Embiids—an agreement extending even to the minutest details! Thus, the anterior transverse region *Pt* in the pronotum of *Grylloblatta* (Fig. 9) finds its counterpart in the region designated as *Pt* in the pronotum of *Embia* (Fig. 6), the epimeron *Em* is very similar in both insects, and in the episternal region of both *Embia* and *Grylloblatta*, there is marked off a sclerite labeled *e*, which is demarked by a curved suture in the two insects.

In *Grylloblatta* and *Embia* the "eutrochantin" *abc* (Figs. 9 and 6) is very similar, and is divided in the same fashion into regions *a*, *b* and *c*, essentially the same in both insects, even to the subdivision of the region *a* by an oblique suture, which, however, is not as distinct in *Embia* as in *Grylloblatta*. Furthermore, the laterosternite *v* of *Embia* (Fig. 6) is represented in *Grylloblatta* (Fig. 9) by a sclerite *v* of exactly the same nature, although it is more closely connected with the sternum *St* in *Grylloblatta* than in *Embia*. On the other hand, these sclerites in both insects are very different from those of the Blattids (Fig. 2).

In the neck region also there is a very close correspondence in the cervical sclerites of the two insects. Thus, the region designated as *s* in *Grylloblatta* (Fig. 9) is represented by a region designated by the same letter in *Embia* (Fig. 6), and the lateral cervical sclerite labeled *i*, with its partially detached portion, labeled *o*, is astonishingly similar in both insects, even to the presence in plate *i* of a longitudinal suture (to which extends the broken line from the letter "i") which is present in but few insects other than the Grylloblattids and Embiids. We find no such agreement between the Grylloblattids and Blattids, and the more features one examines in the insects in question, the more it becomes apparent that the Grylloblattids have practically nothing in common with the Blattids, and practically everything in common with the Embiids. The similarity between the Grylloblattids and the Embiids, (and the dissimilarity between the Grylloblattids) extends to the other structures of the body as well, as will be discussed in a series of papers dealing with these subjects, and these remarkable similarities between the Grylloblattids and Embiids (with the resulting dissimilarities between Grylloblattids and Blattids) must be explained before one can claim that the Grylloblattid line of development is to be traced back to Blattid-like rather than to Embiid-like ancestors, (and through the Embiid-like ancestors, to Plecoptera-like forebears).

The contour of the head is quite similar in the Phasmid *Timema* (Fig. 8) and *Grylloblatta* (Fig. 9), the character of the

neck plates *i* and *o*, and the region labeled *s* is much the same in both insects, but the remainder of the prothorax is somewhat different in the two forms. In regard to the pleural sclerites, and particularly in the character of the plate *abc* (Fig. 8) *Time-ma* resembles certain Plecoptera, but, since I have been unable to obtain the Plecoptera I wished to use for this comparison, I would leave the discussion of the condition found in these insects, until the needed material is available for illustration. In connection with a study of the relationships of the Phylliids, I have recently been able to compare males of *Phyllium scythe* with the flattened Phasmids *Ectatosoma*, and this comparison has shown me that my former views that the Phylliids represent a distinct order, are too extreme. I would, therefore, now regard the Phylliids as a suborder of the Phasmid group, rather than as representing a distinct order, as I have stated in an article dealing with the antennae of the Grylloblattids and Embiids and the relationships of the Orthopteroid insects.

With regard to the relationships between the Forficuloid insects and other lower Pterygota, as indicated by a study of the head, neck and prothoracic regions, the lack of suitable Plecopteron material for comparison with the Forficulids makes it unprofitable to attempt to show the relationships of these two groups of insects at this time. A study of the body structures in general, however, has convinced me that the Forficulids are closely related to the Plecoptera, which doubtless represent as nearly as any living insects the common ancestral stock whence sprang the Forficulid and Embiid lines of development, and these studies indicate more and more clearly that the Blattids do not stand near the direct line of descent of the Orthopteroid forms, but comprise an offshoot arising from the main Pterygotan stem at a comparatively early period of phylogenetic development.

The Forficulids, as exemplified by the rather primitive genus *Echinosoma* (specimens of which were very kindly furnished me by Mr. C. C. Gowdey), are structurally quite similar to the Embiids and Grylloblattids. The head contour is not essentially different in the three groups (Figs. 5, 6, and 9), and the location

of the eyes, antennae, etc., are much the same in all three. (Compare also Fig. 4.) In the neck region of the Forficulid (Fig. 5) there occur two ventral plates *Ps* represented by two similar plates designated as *Ps* in *Embia* (Fig. 6; compare also Fig. 7). The lateral neck plates *i* and *o* are essentially the same in the Forficulid (Fig. 5) Embiid (Fig. 6) and Grylloblattid (Fig. 9), but a rather deep longitudinal fold of the integument in the plate designated as *i* in the Forficulids, presents a modification not met with in the other insects mentioned. In the prothoracic region, sclerite *e* of Fig. 5 is quite like its homologue designated as *e* in Figs. 6 and 9, and the components of plate *abc* are very similar in all three insects, thus indicating a close relationship in the three groups.

A study of the head, neck and prothoracic regions of the Termites reveals points of resemblance to the Blattids on the one hand, and to the Embiid-Forficulid-Grylloblattid "coterie" on the other. I have no specimens of the more primitive Termites, but an examination of the heads of specimens of Termites taken in the Carolinas, of a *Termopsis* from Arizona, and of *Termes bellicosus* from Africa (Fig. 3) would indicate that the prognathous condition is the original one for the group as a whole, although there is a marked tendency for the head to assume a more vertical position—a tendency which has been carried much further in the Blattids (Fig. 2), eventually producing a head of the opisthognathous type in the latter insects.

The contour of the upper portion of the Termite head suggests Blattid affinities, but the location of the eyes, antennae, etc., is more like the condition found in the other insects studied. The neck plates *i*, *i*, and *o* (Fig. 3) are extremely like those of the Blattids (Fig. 2), and the shape of the epimeral region *Em* is much the same in Figs. 3 and 2. The "eutrochantin" *abc* (Fig. 3), however, is not like the trochantin *a* of the roach (Fig. 2), since this region in the roach does not completely intervene between the coxa and the pleural region. The lower portion of the region *a* becomes detached in both insects (Figs. 3 and 2) however, thus indicating a tendency common to

the two groups in this respect. On the other hand the general appearance of the region *abc* of the Termite (Fig. 3) is much more like that of a Phasmid (Fig. 8) or Plecopteron (Fig. 7). A study of the head, neck and prothoracic regions would thus indicate that the Termites are quite closely related to the Blattids, but have retained many characters suggestive of affinities with the other groups studied, and the Termites may thus be regarded as occupying a position somewhat intermediate between the Blattids and the other groups.

It would be inadvisable to base one's conclusions as to the relationships of the lower insects on a study of the head, neck and prothoracic regions alone, and the present paper is therefore but one of a series in which the different body regions have been compared part by part in the different groups; but I am hoping to show that a study of the other structures will in a large measure bear out the conclusions to be drawn from the regions here discussed. Other investigators would derive the Orthopteroid insects from Blattid-like forebears, and would also trace the Grylloblattid line of development back to a Blattoid ancestry; but it is only fair to demand that they shall produce equally convincing proof of their contentions, which should be drawn from the facts of comparative anatomy, since comparative anatomy, after all, furnishes us with the most reliable evidence of relationships, and is, in fact, the main-spring of all systematic work!

Before leaving the subject of the head structures, I would call attention to the antennifer, or antenna-bearing process *Af* which is usually situated midway up the outer portion of the antennal ring *An* in the Grylloblattids, Forficulids, etc. (Figs. 4, 5, etc.), while in the Blattids (Fig. 2) it has migrated mesalward, and in most of the members of this group (e. g. *Ectobia*, etc.) this antenna-bearing process is usually located higher up along the median portion of the antennal ring (i. e. on the side of the antenna toward the median line of the head). The position of the antennifer, however, is not sufficiently constant to be of any great value in determining the relationships of the groups in question.

Another feature which is quite similar in the Phasmids and Grylloblattids, but which is not sufficiently constant in outline to furnish a character of phylogenetic value, is the mandibulare *Bm* (Figs. 9 and 8), or mandible-bearing sclerite. Comstock, 1903, homologizes this sclerite with the trochantin of the leg of the thoracic segments, but it is more than doubtful that such a greatly reduced structure as the trochantin usually is, would be preserved in the mandibular segment. I would be much more inclined to regard this sclerite as representing the coxa of the mandibular appendage, but such speculation is not very profitable until one has carefully compared the mandibles of the Apterygota, Chilopods, Isopods, and lower Crustacea, in which the mandibles become successively more and more leg-like—a comparison which I have not yet had time to carry out. Furthermore, I am not yet prepared to say that the basal segment of the mandible of *Lepisma* (i. e. the portion of the mandible between the terminal portion *Md* and the trophi-bearing sclerite *Tf*, in Fig. 1) is the homolog of the mandibulare *Bm* of the Plecopteron nymph (Fig. 4), since several possibilities suggest themselves (e. g. the region immediately above the mandible in Fig. 1 may represent *Bm*) in comparing the head regions near the mandibles, in the two insects. In order to determine this point, it will be necessary to study a series of Plecopteron and Ephemeropterid nymphs, examining the musculature in each case, since the musculature furnishes many valuable clues in an attempt to homologize the various parts of a metamere or appendage.

A study of an extremely interesting series of heads, including the principal Apterygotan types, the Chilopods, Symphyla, Isopods, etc., has convinced me that the Isopods, Apterygota and "Myriopoda" (*sensu lato*) are very closely related and were derived from similar forebears. Since the Isopods were probably descended from ancestors resembling the sessile-eyed Arthrostraca (such as *Koonunga*, etc.), I would consider these Arthrostraca as very near to the common ancestors of Isopods, Insects, and "Myriopods." The Arthrostraca, in turn, were derived from ancestors similar to the Copepods

and Apodidae, and at the bottom of this stem, the Trilobites unite with the Crustacea, so that it is not surprising that certain Trilobite features might have been retained in some of the groups derived from their common ancestral forms. My own observations would lead me to consider the closely related Insects, Isopods, and "Myriopods" as derived from Arthrostraca-like ancestors, which in turn were derived from lower Crustacean forms ultimately related to the Trilobites, rather than to regard insects, etc., as descended more directly from Trilobite forebears, as certain recent investigators would maintain is the case. These points, however, can be more profitably discussed elsewhere.

The more intimate relationships of the insects considered in the foregoing discussion may be expressed by grouping them into three superorders as follows: The Blattoid, Mantoid, and Isopterous insects form one superorder (the **Pandictyoptera**), in which the head is typically (though not always) hypognathous, the lateral cervicals touch in the median ventral line, and the ventral cervicals, when present, are situated far forward, and occur as two narrow transverse bands somewhat crescent-shaped in outline. A fold of the posterior margin of the tergum projecting backward in two more or less pointed projections (the postplica) usually occurs in both meso- and metathoracic terga, and when the scutellum is demarked, it is usually narrow and extends far forward into the scutal region. The mesothoracic coxae are usually much longer than broad, and the tarsi are typically pentamerous. Ovipositor present in some, absent in others. Styli present in some males.

The Embioid, Forficuloid and Plecopterous insects form the second superorder, the **Panplecoptera**, in which the head is typically prognathous, the lateral cervicals do not touch in the median ventral line, and the ventral cervicals instead of occurring as narrow transverse bands situated far forward in the neck region, are much broader and the posterior one occurs just in front of the prosternum. The mesothoracic coxae are usually as broad as long, tending to have a ring-like outline when viewed from the mesal surface, and the tarsi are typically trimerous. Ovipositor and styli usually absent.

The Grylloblattoid, Phasmoid and Orthopterous insects form a third superorder (the **Panorthoptera**), in which the head is frequently hypognathous, and the lateral cervicals usually do not touch in the median ventral line. The ventral cervicals are usually absent, but when present may be of either of the types mentioned above. The tarsi, typically pentamerous, may be reduced to four or three segments, though a series of five pads on the ventral surface is frequently retained, indicating that the pentamerous condition has not been long lost. The group is typically an ovipositor-bearing one and styli frequently occur in males. All of the insects previously mentioned belong to a single section (the Plecopteradelphina) connected by intermediate or annectant forms, and apparently descended from ancestors not very different from recent Plecoptera.

Since sending the foregoing discussion to the editor of the "News" an extremely important paper by Pantel, 1917 ("A Proposito de un Anisolabis Alado" in: Mem. R. Acad. Cienc. y Artes, Barcelona), has been published, in which he figures a series of Dermaptera including *Allostethus*, *Labidura* and *Anisolabis*, which furnishes an unusually clear illustration of the gradual fusion of the posterior portion of the eutrochantin (Fig. 5, *bc*), with the lower portion of the prothoracic pleuron, while the anterior portion of the eutrochantin (Fig. 5, *a*), remains free to form the so-called trochantin of the higher forms, thus offering a very conclusive demonstration of the claim made in a preceding discussion concerning the fusion of the posterior portion of the eutrochantin with the lower portion of the pleural region, etc.

In the appended list the abbreviations used in Plate XXVII are quite fully explained, so that it is unnecessary to discuss further the additional points of similarity in the groups of insects here shown, since homologous structures bear the same label throughout the series.

ABBREVIATIONS.

a, b, c—Sclerites composing the trochantin-like region called the eutrochantin, which intervenes between the coxa and the pleural

region in the Apterygota, and in the prothorax of the lowest Pterygota. In Fig. 2, *a* is the trochantin, from which the so-called trochantinelle has become detached.

Af—Antennifer, or antenna-bearing process.

An—Antennale, or ring at base of antenna.

At—Antenna, only portion of basal segment shown.

Bm—Mandibulare, or sclerite at base of mandible.

Cl—Clypeus.

c—Curvipleurite, or curved pleurite marked off in the episternal region.

Em—Epimeron.

i—Laterocervicale, or lateral cervical sclerite, divided into two parts in Figs. 2 and 3, the sclerite *o* being marked off in the posterior part.

L—Labium. Only basal portion shown.

Lb—Labrum.

Md—Mandible.

Mx—Maxilla. Only basal portion shown.

o—Posterior portion of lateral cervical sclerite.

Pc—Paracephal suture.

Pn—Pronotum.

Ps—Two ventral cervical sclerites, the anterior of which is the intersternite, and the posterior one is the presternite, excepting Fig. 2.

Pt—Pretergite, or anterior transverse region of tergum.

s—Region in front of prothoracic epimeron, probably homologue of the lateropleurite of other segments.

St—Sternum of prothorax.

Tf—Trophifer, or trophi-bearing segment to which all three of the mouthparts are articulated in Fig. 1. It is a portion of the occipital region.

v—The laterosternite in Figs. 5, 6, 7 and 9. In others it is a region connecting sternum with pleuron.

x—Small plate in front of dorso-pleural region.

z—Dorsal cervical sclerite, or intertergite.

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